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## **Atypical Early Histories Predict Lower Extraversion in Captive Chimpanzees**

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### **Abstract**

There are still gaps in our understanding of personality development in humans, particularly in relation to social influences. Chimpanzee personality development may provide useful insight. We evaluated the impact of early life experiences on personality development by studying 88 chimpanzees living in accredited zoos and sanctuaries. During infancy, subjects varied in the amount of time spent with conspecifics compared with humans. Caregivers familiar with the chimpanzees rated them using a modified version of the Hominoid Personality Questionnaire (HPQ). The ratings were found to have strong inter-rater reliability. We used the six-factor structure of the HPQ to evaluate our results in relation to differences in early life experience. Chimpanzees who as infants were less exposed to conspecifics were rated as lower in Extraversion later in life. These results suggest that a broader range of social influences should be considered when evaluating the impact of early social environment on later personality expression.

*Keywords:* [chimpanzees, personality, early life, social environment, Extraversion]

### **Atypical Early Histories Predict Lower Extraversion in Captive Chimpanzees**

There has been growing interest in determining the relative influence of several factors on the development of human personality (de Haan, Delović, van den Akker, Stoltz & Prinzie, 2013; McFarlane et al, 2005; Roy, 2002). The impact of families and parents appear particularly influential but the mechanisms behind social and environmental interactions remain poorly understood (Lemery-Chalfant, Kao, Swann & Hill Goldsmith, 2013). Studies that focused on the joint influence of environment and genetics in humans have yielded varied results in terms of which personality factors are impacted and how they are impacted. A review by Burt (2008) found that under conditions of poor parenting, negative emotionality is more influenced by the environment than by genetics. In addition to these findings, there were no clear results for impulsivity, an aspect of negative emotionality related to externalizing disorders. Another study found that unsafe conditions in the home environment were significantly related to negative affectivity, more chaotic home environments were related to higher extraversion, and that both of these effects were genetically mediated (Lemery-Chalfant et al. 2013). Other demographic factors may also be influential. For example, Nakao et al. (2000) reported that the impact of family environment varied across different personality factors and across socioeconomic classes.

In addition to the potential impact of early life events on the normal range of personality traits, it is clear that particularly stressful events, can lead to the differential expression of personality and potentially, clinical personality disorders (Lahti et al., 2012; Sullivan, Neale & Kendler, 2000). For example, parental separation is associated with greater risk for clinical disorders, such as borderline personality disorder (Lahti et al., 2012) and major depressive episodes (Sullivan et al., 2000). In addition, a combination of overprotectiveness on the part of the mother and an absent father has been shown to result in an increased risk for anxious and

schizotypal personality factors associated with these disorders (Giakoumaki et al., 2012). To advance the treatment of a range of such disorders there is a need for a greater understanding of the connection between early life experiences, personality, and developmental consequences. One way in which this understanding can be deepened is by conducting investigations of other species.

Although there is a growing literature on the influence of early environment on human personality development, there are few studies on nonhuman primates. Most studies have been on macaques and focused on the short-term effects of differential rearing conditions (Caine, Earle & Reite, 1983; Clarke & Snipes, 1998; Harlow & Harlow, 1969; Stevenson-Hinde, Stillwell-Barnes & Zunz, 1980; Suomi, 1987). For instance, Caine (1983) found that pig-tailed macaques who were briefly separated from their mothers were rated as less sociable two years later compared with those who were not separated from their mothers. In addition, Clarke and Snipes (1998) examined the impact of peer rearing compared to mother rearing on personality development in macaques and found that peer-reared individuals were rated as more social and more focused on the environment at an early age.

Though most non-human primate studies investigating the relationship between personality and early history have focused on macaques, chimpanzees are an excellent model for addressing questions of personality and development due to their close evolutionary relationship to humans and the range of complex social needs that influence their well-being (de Waal & Aureli, 1996). Studies of chimpanzees have revealed mixed findings in relation to the influence of rearing history on personality. Bard and Gardner (1996), Murray (1998) and Latzman, Freeman, Schapiro and Hopkins (submitted) found that rearing history had an impact on personality, though these studies differed in terms of sample sizes, setting, and degree to which

wild-born subjects were considered. Conversely, studies by Martin (2002, 2005) found no such relationship between rearing and personality. These varying results underscore the need for continued research and an approach that factors in the widest possible range of influences. The results of such research would aid not only in our comprehension of personality ontogeny but also the phylogeny of human personality development and the potential for management tools with which to address the well-being of captive nonhuman primates.

To investigate the impact of social influences on the development of chimpanzee personality we collected personality ratings from chimpanzees living in accredited zoos and sanctuaries across the United States. These individuals had a range of early histories. Some subjects were raised in their natal group throughout their lives and were thus primarily exposed to other chimpanzees. Other subjects had less typical early histories, having spent some period of their lives as personal pets or trained performers for the entertainment industry, and were thus primarily exposed to humans.

To examine the impact of early social history, we devised a continuous measure of exposure to chimpanzees and humans: the Chimpanzee-Human Index (CHI; Freeman & Ross, 2014). Using this index we examined the effect that typical (chimpanzee) and atypical (human) exposure had on personality traits measured later in life. Specifically, we focused on the developmentally important period of infancy to best capture the long-term impact of early social environmental effects. Based on the findings of previous studies (Clark & Snipes, 1998; McFarlane et al., 2005) we predicted that particular personality factors, specifically neuroticism, openness, and extraversion, would be related to differences in early social exposure.

## Methods

## **Subjects**

Subjects were 88 captive-born chimpanzees (34 males and 54 females) ranging in age from 3 to 54 years (mean age  $\pm$  *SD* = 20.5  $\pm$  10.3). None of the chimpanzees were wild born and none had lived in a laboratory environment. Subjects varied in the degree of human and conspecific exposure they experienced in early life (Freeman & Ross, 2014). Thirty-six subjects were formerly owned as personal pets or trained performers but had subsequently been moved to zoos or sanctuaries.

Subjects were evaluated in their current housing at member sanctuaries of the North American Primate Sanctuary Alliance (NAPSA: Center for Great Apes, Chimps, Inc. and Save the Chimps) or zoological parks accredited by the Association of Zoos and Aquariums (AZA: Dallas Zoo, Henry Vilas Zoo, Houston Zoo, Knoxville Zoo, Lincoln Park Zoo, Lion Country Safari, Little Rock Zoo, North Carolina Zoo, Oakland Zoo, Oklahoma City Zoo, Oregon Zoo, Riverside Discovery Center, Sunset Zoo and Tulsa Zoo). Care and housing of individuals met the accrediting standards of either the Association of Zoos and Aquariums (AZA) or the Global Federation of Animal Sanctuaries (GFAS).

Eighty-seven subjects were socially housed with between 1 and 25 chimpanzees (mean group size = 7). The one individually housed chimpanzee was kept as a solitary pet for over 30 years and attempts to introduce her to conspecifics have not been successful.

This study complied with protocols approved by the Chimpanzee Species Survival Plan (SSP) management group and animal care committees at each participating institution.

## **Instrument**

We used the Hominoid Personality Questionnaire (HPQ<sup>1</sup>; Weiss et al., 2009) to collect personality ratings. The HPQ consists of 54 adjectives, each paired with a definition that sets the

adjective in the context of primate behavior. The HPQ was developed from the 48-item Orangutan Personality Questionnaire (Weiss, King & Perkins, 2006), which was an expanded version of the 43-item Chimpanzee Personality Questionnaire (King & Figueredo, 1997). Of the 43 adjectives in the Chimpanzee Personality Questionnaire, 41 were sampled from Goldberg (1990) taxonomy of the Big Five. For this study, we modified the HPQ by including three items that were identified in a previous study (Freeman et al., 2013): sexual, human oriented, and self-caring.

### **Raters and Ratings**

Questionnaires were distributed to between two to six caregivers (mean = 3.5) who regularly worked with the chimpanzees. Raters were asked to rate each chimpanzee on each item based on all of their experiences with that individual. Ratings were made on a seven-point scale with 1 indicating that the subject “displays either total absence or negligible amounts of the trait” and 7 indicating that the subject “displays large amounts of the trait”. Raters were instructed to not discuss their ratings with others until all questionnaires were submitted.

### **Chimpanzee Human Interaction Index**

Details about the CHI are presented in Freeman and Ross (2014). The CHI is a continuous measure that quantifies the degree of exposure to potential social influences (conspecifics and humans) each chimpanzee has had throughout his/her life. It was calculated by using management records acquired from past and current holding institutions to calculate the proportion of time per day that each chimpanzee spent in each of three categories: full exposure to conspecifics, full exposure to humans, and exposure to both conspecifics and humans. Each day was weighted based on each of these categories such that a score of 1 indicated they spent all their social time with other chimpanzees and a score of 0 indicated they spent all of their social



time with humans. A score of 0.5 indicated a mix of human and chimpanzee exposure. For this analysis, we focused on social exposure during the first four years of life. As such, we summed the daily scores and divided the total by the number of days in four years (1460) to give the final CHI value during infancy ( $CHI_i$ ) for each individual. A higher  $CHI_i$  value indicates more exposure to other chimpanzees and a lower  $CHI_i$  value indicates more exposure to humans.

## **Results**

### **Inter-rater Reliability**

We computed inter-rater reliabilities using intraclass correlations (*ICCs*, Shrout & Fleiss, 1979). The first,  $ICC(3,1)$ , indicates the reliability of individual ratings. The second,  $ICC(3,k)$ , indicates the reliability of mean scores based on  $k$  raters. Inter-rater reliabilities for all traits are presented in Table S1.  $ICC(3,1)$  for the traits ranged from .01 (Unemotional) to .15 (Sexual) (mean = .09). The  $ICC(3,k)$ s for the traits ranged from .30 for predictable to .85 for sexual (mean = .63), and thus were reliable and comparable to previous studies (Gosling, 1998; King & Figueredo, 1997).

### **Factor Scores**

Using the definitions of Weiss et al. (2009), we created unit-weighted factor scores for the Agreeableness, Conscientiousness, Dominance, Extraversion, Neuroticism, and Openness factors. We then transformed these scores into  $z$ -scores.

### **Factor Score Reliabilities**

We computed inter-rater reliabilities of the factor scores using intraclass correlation coefficients. The results for each of the scales are as follows, with  $ICC(3,1)$  followed by  $ICC(3,k)$ : Agreeableness (.31, .73), Conscientiousness (.27, .84), Dominance (.48, .94), Extraversion (.43, .88), Neuroticism (.16, .48) and Openness (.75, .92). The internal consistency

reliabilities (Cronbach's alphas) for these scales are as follows: Agreeableness (.73), Conscientiousness (.84), Dominance (.94), Extraversion (.88), Neuroticism (.48), and Openness (.92). The inter-rater reliabilities and internal consistencies of these scales are comparable to those found for personality factors in humans (e.g., John & Robins, 1993), chimpanzees (e.g., King & Figueredo, 1997), and other nonhuman primates (e.g., Capitanio, 1999).

### **Genetic Relationships between Individuals Housed Together**

Although some of the individuals living together in their current institutions are related to each other, the effective sample size was 65. Thus, the degree of non-independence stemming from relatedness was slight. However, to guard against this non-independence, we examined whether any effects were still significant after adjusting the error degrees of freedom.

### **Association of Personality with CHI scores**

Table 1 shows results from six multiple regressions where personality factor scores were entered as dependent variables. Sex was entered as a categorical variable and age and  $CHI_i$  were entered as continuous variables. Age was centered before being entered in the model. The model also included the  $Age \times CHI_i$ ,  $Sex \times CHI_i$ ,  $Sex \times Age$ , and  $Age \times Sex \times CHI_i$  interaction terms.

Extraversion was positively associated with  $CHI_i$ ,  $F_{1,87} = 10.24$ ,  $p = .002$ . This effect was still significant after adjusting the error degrees of freedom to reflect the effective sample size ( $F_{1,64} = 10.24$ ,  $p = .002$ ) and, regardless of whether the total or effective sample size was used to generate  $p$ -values, correcting for multiple tests using the Bonferroni procedure (adjusted critical  $p = .008$ ). The main effects of age and sex and the  $Age \times CHI_i$ ,  $Sex \times CHI_i$ ,  $Sex \times Age$ , and  $Age \times Sex \times CHI_i$  interactions were not significant. It should be noted that although the parameter estimate for  $Age \times CHI_i$  differs from zero, it does not account for significant portion of the variance. In total the model accounted for approximately nearly half of the variance in

Extraversion,  $R^2 = .464$ , adjusted  $R^2 = .417$ . None of the other personality traits were significantly associated with any of the predictors or their interactions.

### **Discussion**

Captive chimpanzees in the United States have a range of early life histories and variable exposures to both conspecifics and to human caregivers. We leveraged this variability to determine whether early experiences impact personality development and found that less frequent early exposure to conspecifics was associated with lower Extraversion later in life. This finding supports the links between differences in early environment and personality that has been found in humans (Lemery-Chalfant et al., 2013; McFarlane, et al., 2005; Nakao et al., 2000; Roy, 2002) and is consistent with earlier studies that suggest that rearing history impacts nonhuman primate personality development (Clark & Snipes, 1998; Latzman et al., submitted; Murray, 1998). These data add to evidence that suggests the critical nature that the social environment, has on personality development.

The current findings imply that compared to other personality factors, Extraversion might have evolved so as to require early input from the social environment and indeed the association between early environment and Extraversion has been found in studies of humans (Lemery-Chalfant et al., 2013; Nakao et al., 2000). A recent study investigating the link between chimpanzees and early rearing history also found a significant relationship between early history and Extraversion in which the effect was in the opposite direction; human-raised individuals had higher Extraversion scores compared with those who were mother-raised (Latzman et al., submitted). One possible explanation for this difference could be that one of the strongest items on the Extraversion factor for this study was “Human oriented”, indicating the chimpanzees were focused more on humans than other chimpanzees.

The few other studies investigating the link between chimpanzee personality and early history also found differing results, although none of them measured Extraversion specifically. Bard and Gardner (1996) found that chimpanzees with the most stressful early history exhibited differences in emotions and coping styles compared with chimpanzees with less stressful early histories. Murray (1998) found that human-reared chimpanzees were rated higher on the traits effective, protective, and eccentric as adults, but these adjectives are not related to Extraversion. Martin did not find a relationship between early history and personality in chimpanzees (Martin 2002, 2005). One reason why our results may differ from those of Murray (1998) and Martin (2002, 2005) is that we assessed the early history of the chimpanzees using a larger samples size and a continuous metric that incorporated more details about the degree of potential interaction with both conspecifics and humans. It is possible that this broader measure of early life experiences that encompasses the impact of a range of influences may be better suited for studying the impact of early life on personality development in chimpanzees and other nonhuman primates.

In combination with an earlier analysis of this population of chimpanzees we continue to augment our understanding of the associated personality and behavioral outcomes related to early social exposures. In that study, we found that chimpanzees with low conspecific exposure during infancy displayed low levels of grooming, a critical behavior in terms of social cohesion, as adolescents or adults (Freeman & Ross, 2014). It is not surprising then, that these same low-CHI chimpanzees are rated lower in Extraversion and this relates well to studies that have determined links between personality ratings and patterns of social behavior. In addition, Massen and Koski (2013) determined that chimpanzees favored interactions with other

chimpanzees who has similar scores on a factor labeled Sociability. In addition, zoo-housed chimpanzees rated higher on Extraversion were found to spend more time engaging in Affinitive behaviors and less time at the public viewing window around human visitors (Pederson, King & Landau, 2005).

These findings are potentially relevant in terms of assessments of the welfare impact of early histories. Previous studies found that Extraversion is related to long-term welfare outcomes in humans and nonhuman primates. Extraversion scores have been shown to be related to ratings of subjective well-being in both humans and nonhuman primates (humans: Steel, Schmidt & Shultz, 2008; orangutans: Weiss et al., 2006; chimpanzees: Weiss et al., 2009). Likewise, higher scores on Extraversion have been shown to predict longer life spans in gorillas (Weiss, Inoue-Murayama, King, Adams & Matsuzawa, 2013) as well as stronger immune responses in rhesus macaques (Capitanio, 2011).

This study gives support to the idea that early histories impact long-term personality development in chimpanzees in a similar way to how early histories in humans have been shown to also impact long-term personality development (Lemery-Chalfant et al., 2013; Nakao et al., 2000). Although this study focused on personality factors in chimpanzees that are within the normal range of variability, increasing knowledge about the long-term consequences of early history in chimpanzees could broaden our understanding of clinical personality disorders in humans as well.

There are some limitations with this study. Although we accounted for the degree of genetic relatedness in our sample with our analyses, we were not able to take into consideration the separate impact of genetics and early history on long-term personality. Given that a recent study by Latzman et al. (submitted) found links between vasopressin and personality differences

in chimpanzees, future research should encompass more investigation of the combination of genetics and early history in relation to the long-term impacts on personality. Another potential limitation was that although each facility was accredited and provided high quality care and management, there are some differences in care protocols across settings that have the potential to confound the findings. These include differences in diet, physical environment, enrichment, and management styles. For example, some facilities had more frequent interactions with the chimpanzees. However, these differences are unlikely to account for our findings as previous studies have not found evidence for the impact of differences such as physical and social attributes between zoos on personality (Weiss, King & Figueredo, 2000; Weiss & King, 2006).

This study informs our understanding about the relationship between early social environments and later personality factors. It is important to investigate the implications of this relationship further, particularly in relation to situations where social environments change drastically across an individual's life. In relation to chimpanzees, and specifically those who spent more time with humans than chimpanzees, the personality differences found in connection with behavioral differences (Freeman & Ross, 2014) provide more evidence that early exposure to conspecifics is important for the normal development of chimpanzee personality and the long-term welfare of these individuals.

### **Author Contributions**

This study was designed by SRR in collaboration with HDF. HDF coordinated the collection of the personality ratings at each of the facilities. HDF analyzed the data with advice from AW. HDF, AW and SRR contributed to the writing of this article.

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### **Footnotes**

<sup>1</sup>The Hominoid Personality Questionnaire is freely available at

[http://extras.springer.com/2011/978-1-4614-0175-9/weiss\\_chimpanzee\\_personality.pdf](http://extras.springer.com/2011/978-1-4614-0175-9/weiss_chimpanzee_personality.pdf).

Table 1

*Association of Chimpanzee Human Index Infant (CHI<sub>i</sub>) Scores with Personality Factors*

							95% <i>CI</i>	
	Type III Sum of Squares	Df (test,error)	F	p-value	<i>b</i>	<i>s.e.</i>	lower	upper
Agreeableness								
Intercept	242.868	1, 87	586.178	<.0001	4.300	0.224	3.855	4.745
Sex	.108	1, 87	.261	.611	-0.178	0.348	-0.870	0.515
Age	.087	1, 87	.210	.648	-0.020	0.015	-0.050	0.010
CHI <sub>i</sub>	.084	1, 87	.202	.654	-0.119	0.313	-0.742	0.504
Sex × CHI <sub>i</sub>	.001	1, 87	.002	.962	0.023	0.478	-0.929	0.974
Age × CHI <sub>i</sub>	.236	1, 87	.569	.453	0.021	0.025	-0.028	0.069
Sex × Age	.109	1, 87	.262	.610	0.021	0.041	-0.061	0.102
Sex × Age × CHI <sub>i</sub>	.001	1, 87	.001	.972	-0.002	0.052	-0.105	0.102
Conscientiousness								
Intercept	197.599	1, 87	509.655	<.0001	3.920	0.216	3.490	4.350
Sex	.203	1, 87	.523	.472	-0.243	0.336	-0.913	0.426
Age	.066	1, 87	.171	.680	0.002	0.014	-0.027	0.031
CHI <sub>i</sub>	.270	1, 87	.697	.406	0.073	0.303	-0.530	0.675
Sex × CHI <sub>i</sub>	.105	1, 87	.271	.604	0.241	0.463	-0.680	1.161
Age × CHI <sub>i</sub>	.050	1, 87	.128	.721	-0.017	0.024	-0.064	0.031
Sex × Age	.099	1, 87	.255	.615	-0.020	0.040	-0.099	0.059
Sex × Age × CHI <sub>i</sub>	.404	1, 87	1.042	.310	0.051	0.050	-0.049	0.152

Dominance								
Intercept	176.358	1, 87	215.454	<.0001	3.352	0.314	2.727	3.978
Sex	.762	1, 87	.931	.338	0.472	0.489	-0.501	1.445
Age	2.234	1, 87	2.730	.102	0.024	0.021	-0.018	0.066
CHI <sub>i</sub>	.929	1, 87	1.135	.290	0.448	0.440	-0.428	1.323
Sex × CHI <sub>i</sub>	.058	1, 87	.071	.790	-0.180	0.672	-1.517	1.158
Age × CHI <sub>i</sub>	1.068	1, 87	1.305	.257	0.005	0.035	-0.064	0.074
Sex × Age	.537	1, 87	.656	.420	0.047	0.058	-0.068	0.161
Sex × Age × CHI <sub>i</sub>	1.338	1, 87	1.635	.205	-0.094	0.073	-0.239	0.052
Extraversion								
Intercept	181.240	1, 87	453.212	<.0001	3.384	0.220	2.947	3.821
Sex	.882	1, 87	2.206	.141	0.508	0.342	-0.173	1.188
Age	.616	1, 87	1.540	.218	-0.007	0.015	-0.036	0.023
CHI <sub>i</sub>	4.093	1, 87	10.235	.002	0.930	0.307	0.319	1.542
Sex × CHI <sub>i</sub>	.232	1, 87	.581	.448	-0.358	0.470	-1.293	0.577
Age × CHI <sub>i</sub>	.550	1, 87	1.305	.257	-0.062	0.024	-0.110	-0.014
Sex × Age	.336	1, 87	.839	.362	-0.037	0.040	-0.117	0.043
Sex × Age × CHI <sub>i</sub>	.627	1, 87	1.568	.214	0.064	0.051	-0.038	0.166
Neuroticism								
Intercept	212.764	1, 87	520.720	< .0001	3.943	0.222	3.501	4.385
Sex	<.0001	1, 87	<.0001	.992	-0.003	0.345	-0.691	0.684
Age	.625	1, 87	1.528	.220	-0.013	0.015	-0.043	0.016
CHI <sub>i</sub>	.616	1, 87	1.540	.218	-0.215	0.311	-0.833	0.404
Sex × CHI <sub>i</sub>	.004	1, 87	.010	.919	-0.048	0.475	-0.993	0.897
Age × CHI <sub>i</sub>	.152	1, 87	.371	.544	0.008	0.024	-0.040	0.057
Sex × Age	.142	1, 87	.347	.557	-0.024	0.041	-0.105	0.057

Sex $\times$ Age $\times$ CHI <sub>i</sub>	.033	1, 87	.082.	.776	0.015	0.052	-0.088	0.118
Openness								
Intercept	266.796	1, 87	310.376	<.0001	4.272	0.322	3.630	4.913
Sex	.274	1, 87	.319	.574	0.283	0.501	-0.714	1.280
Age	1.470	1, 87	1.710	.195	-0.005	0.022	-0.048	0.038
CHI <sub>i</sub>	<.0001	1, 87	<.0001	.994	0.109	0.451	-0.788	1.006
Sex $\times$ CHI <sub>i</sub>	.82	1, 87	.095	.759	-0.212	0.689	-1.583	1.158
Age $\times$ CHI <sub>i</sub>	.338	1, 87	.393	.532	-0.057	0.035	-0.128	0.013
Sex $\times$ Age	1.108	1, 87	1.289	.260	-0.067	0.059	-0.184	0.050
Sex $\times$ Age $\times$ CHI <sub>i</sub>	.696	1, 87	.810	.371	0.067	0.075	-0.082	0.217